Demography and dynamics of the dominant woody species in a communal and protected area of the eastern Transvaal Lowveld

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The size class distributions of the seven most abundant woody species in an area of the Transvaal Lowveld were determined for two contrasting management systems, i.e. communal land and a protected area. Most of the size class profiles indicated that the populations were not stable, experiencing fluctuating recruitment and/or mortality rates. This is probably the norm in semi-arid environments characterized by large fluctuations in the timing and intensity of controlling variables. Communal management reduced absolute densities and altered the size class profile of all but one of the species considered. This was usually manifested as a reduction in the proportion of larger individuals.

Die grootteklasverspreidings van sewe van die volopste houtagtige plantspesies is vir twee verskillende bestuurstelsels in die Transvaalse Laeveld bepaal: gemeenskapsgrond en beskermde area. Die meeste van die grootteklasprofiele het getoon dat die populasies nie stabiel is nie en dat hulle wisselend aanwas en/of afsterf. Dit is waarskynlik die normale proses in semi-ariede omgewings wat gekenmerk word deur groot wisselinge in die skedulering en intensiteit van bepalende veranderlikes. Gemeenskapsbestuur het die absolute digtheid van alle spesies, behalwe een, verminder en die grootteklasprofiel verander. In die meeste gevalle was daar 'n vermindering in die verhouding van die groter individue.

Keywords: Communal, plant demography, quotient, size class, woody species.

Introduction

Characterization of the size and age class distributions of woody species is a useful mechanism for the projection of population trends and, to a lesser extent, past perturbations. Projections of future states of the population also facilitate inferences regarding the stability of woody communities and populations (Harper 1977).

Such work is scarce in southern African savannas, and managers and researchers in this region have little knowledge of the effect of contrasting management practices on the structure and stability of local tree populations. Past and recent efforts concentrate heavily on changes in species composition rather than structure. Yet changes in the latter often occur before species compositional changes (Harper 1977; Pellew 1983), and are therefore useful indicators of the management impact (e.g. Witkowski 1983) before the loss of valuable species occurs. They may also alert managers to situations of declining recruitment, as was reported by Walker *et al.* (1986).

Unfortunately, age class data are unreliable for savanna areas because growth rings are not directly related to age, but are rather a reflection of the fluctuating environmental conditions characteristic of the savanna biome (Lilly 1977). Thus, additional rings may be produced with unseasonal rains, or, in times of drought, no rings will be formed. Moreover, growth rings frequently cannot be identified for savanna species (Lilly 1977; Walker *et al.* 1986), although there are exceptions (Prins & van der Jeugd 1992). This restricts analyses of population structure to size classes. Although this prevents interpretation of past events affecting population structure (Harper 1977), there are suggestions that size class distributions (Werner & Caswell 1977; Knowles & Grant 1983), or stage class distributions (Silvertown 1987) are better indicators of reproductive output than are age classes. Harper (1977) also suggested that size could be of greater significance than age in determining the community structure and mortality or survival of plants.

The aim of this study was to describe and compare the size distributions of the more abundant savanna tree species in a selected area of the Transvaal Lowveld. It addressed two key questions: (i) Are the populations of the more common savanna species in a stable state? (ii) How are the size distributions of common savanna species affected by communal management?

Study area

The study area straddles the boundary between the Republic of South Africa and Gazankulu in the eastern Transvaal Lowveld (midpoint 24°31'S, 31°06'E). Protected woody communities were sampled at Wits Rural Facility on the farm Guernsey (550 ha). This adjoins communal grazing lands on the farm Okkerneutboom in Gazankulu (740 ha).

The area is underlain by Basement Complex strata of the Bandelierkop Complex, typified by potassic granites and grandiorite. The most extensive soil types are shallow lithosols, except towards the base of the catena.

Mean annual rainfall is 670 mm with wide variability from year to year. Nearly all the rain is received during the summer months between October and April, usually in the form of convectional thunderstorms. Mean annual temperature is approximately 22°C. Frost is rare.

The area falls on the boundary of Acocks's (1988) veld types 10 (Lowveld) and 11 (Arid Lowveld). The tree stratum is dominated by *Terminalia sericea, Acacia* spp. and *Combretum* spp. Dominant grasses include *Pogonathria squarrosa, Bothriochloa insculpta, Hyparrhenia* spp., *Heteropogon contortus, Eragrostis gummiflua, Aristida bipartita* and *Cynodon dactylon*. Nomenclature follows that of Gibbs Russell *et al.* (1985).

The communal grazing land has been zoned as such for at least fifteen years. Scattered homesteads existed there previously, indicating that there has been some degree of exploitation for several decades resulting in a clear alteration of community physiognomy, such that it typifies a short sparse woodland according to Edwards's (1983) physiognomic classification. The contrasting unharvested area has not been open to fuelwood harvesting for over 25 years. It is considerably denser in overall appearance and is classified as a short bushland according to Edwards (1983).

However, it appears that there has been selective removal from the protected area of species used in the local, commercial furniture trade (*Pterocarpus angolensis* and *Combretum imberbe*), with few mature individuals of these two species remaining. The protected area has not been burnt for the last two decades and grazing has been very light.

Methods

A co-ordinate system was laid over aerial photographs of each of the sample areas, namely the protected area and the adjacent communal land. Randomly generated sample sites were then marked on the overlay. Each sample in the field was measured from the closest identifiable point to ensure that samples were located according to the distribution on the overlay. Thirty samples were placed in the unharvested area and 40 in the communal grazing lands during April and May 1990.

Each sample comprised a transect of 80 m × 5 m (400 m^2), within which the circumference of each woody stem just above the basal swelling (5 – 50 cm above the ground depending upon the height of the stem) was recorded. Each stem was measured separately for individuals that had coppiced as a result of cutting or had branched at ground level.

Size classes were arbitrarily determined as 5-cm increments in circumference. Thus, size class 1 represented stems ≤5 cm circumference; class 2, 6 – 10 cm; class 3, 11 – 15 cm; and so on (16 – 20 cm; 21 – 25 cm; 26 – 30 cm; 31 – 35 cm; 36 – 40 cm; 41 – 45 cm; 46 – 50 cm; 51 – 55 cm; 56 – 60 cm; 61 – 65 cm; 66 – 70 cm; 71 – 75 cm) up to size class 15. All stems larger than size class 15 were pooled in a single size class.

Results are presented for only those species that had a relative density of >2 % at either of the sites. These seven species constituted 62.7 and 82.2% of the mean number of stems per hectare at the protected and communal areas, respectively, and included species favoured by fuelwood collectors (*Acacia swazica, Combretum collinum* and *Terminalia sericea*) as well as others that are avoided (*Lantana camara, Maytenus senegalensis* and *Strychnos madagascariensis*), and *Dichrostachys cinerea* that has a variable local rating with respect to preference as a fuelwood (Shackleton 1993).

Data were displayed graphically to determine population trends and stability. Plots for each species of mean density per size class enhance interpretation about future trends for a given population (Rao *et al.* 1990). Mean density values (per hectare) were logarithmically transformed (natural logarithm). Quotients were calculated between successive size classes as described by Meyer (1952) and Leak (1964) to facilitate graphical interpretation of population stability. Approximately constant quotients across sampled size classes indicate a stable population, whereas fluctuating quotients indicate an unstable population (Taylor & Walker 1984).

Significant differences in size class profiles (proportions) between the two areas were tested using the chi-squared statistic, with pooling of classes with less than five observations (Sokal & Rohlf 1981).

Stems with a circumference <2 cm were regarded as newly derived stems, indicating regenerative capacity through seed germination and establishment, or through vegetative reproduction. This definition may include stems from previous seasons that had died back during the non-growing season (Chidumayo 1992a,b), but it still provides an index of reproductive capacity.

Results

The mean density of each of the seven species differed markedly between the two sites (Table 1). Densities of *L. camara, M. senegalensis* and *T. sericea* were highest in the communal land, whilst densities of the other four species (*A. swazica, C. collinum, D. cinerea* and *S. madagascariensis*) where highest in the protected area.

The density plots of *A. swazica, C. collinum, D. cinerea* and *S. madagascariensis* at the protected site had a rotated sigmoid curve (Figure 1). This curve was not evident for any of the density plots for species from the communal site. Of the remaining two species from the protected site, *T. sericea* had a reversed J-shaped density curve, characteristic of a stable population (Meyer 1952; Rabotnov 1969; Rao *et al.* 1990), and *M. senegalensis* exhibited a relative linear decline. Such a linear decline was also found for some of the species from the communal area, namely *D. cinerea* and *S. madagascariensis*. Schmeiz and Lindsey (1965) reported that such a decline was typical of uneven-aged mixed populations.

Table 1 Densities (stems/ha ± SE) of the dominant woody species at the protected and communal areas

Species	Protected site (n = 30)	Communal site (n = 40)	p
A. swazica	304.3 ± 87.0	—	
C. collinum	292.5 ± 76.3	33.3 ± 15.3	< 0.0001
D. cinerea	1227.5 ± 219.5	246.3 ± 54.8	< 0.0001
L. camara	—	373.3 ± 126.8	
M. senegalensis	215.0 ± 86.8	567.0 ± 178.5	< 0.0001
S. madagascariensis	321.8 ± 121.5	35.8 ± 12.3	< 0.0001
T. sericea	1116.8 ± 197.8	3027.5 ± 727.0	< 0.0001
Total	3477.9	4283.2	
Other species	2069.0	927.5	

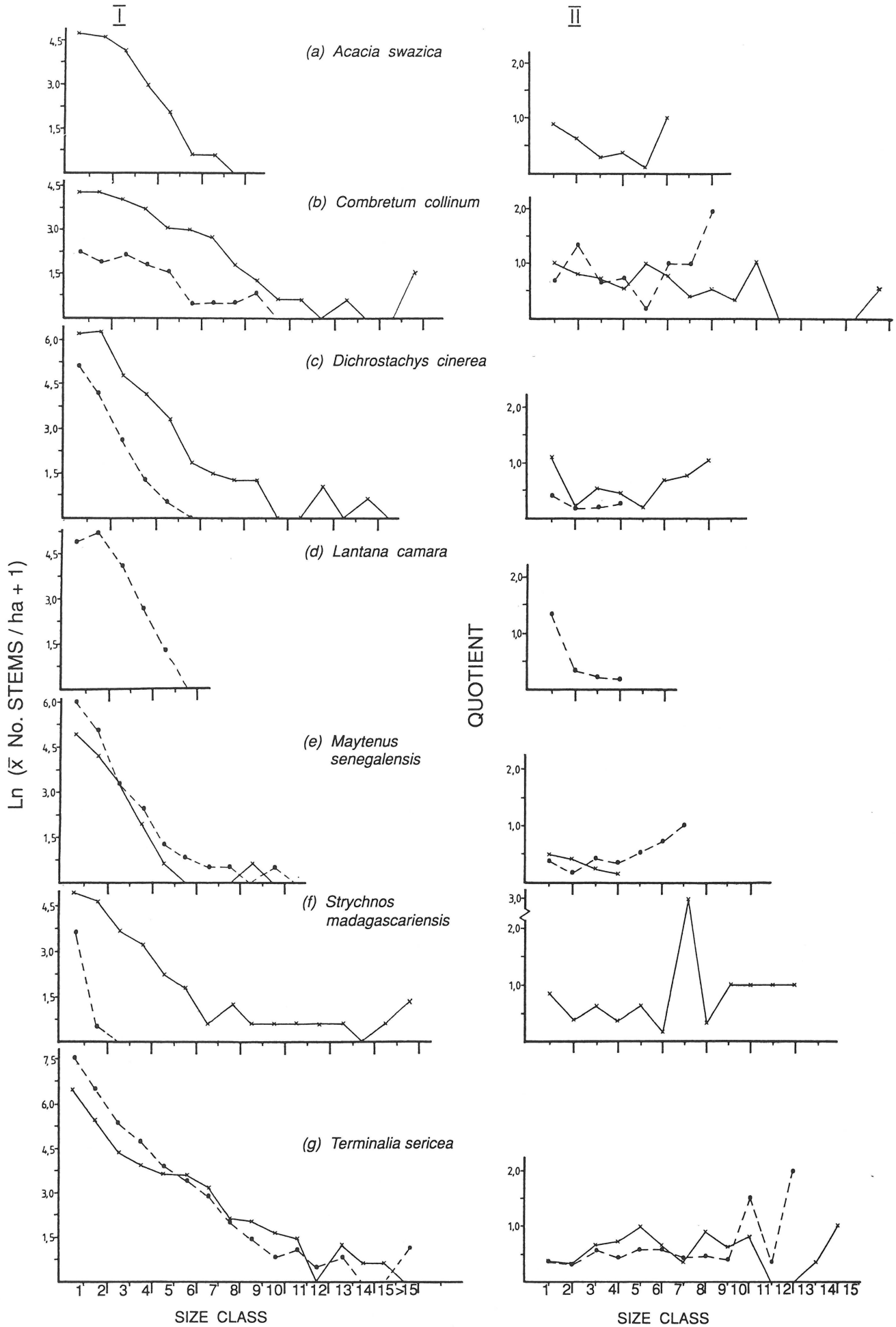

Figure 1 Density (I) and quotient (II) distributions for seven species determined for the protected (——) and communal (– – –) sites.

The other species in the communal land indicated a variable set of density distributions, including a truncated rotated sigmoidal curve (*L. camara*), a flattened rotated sigmoid curve (*C. collinum*), and a standard reversed J-shaped curve (*M. senegalensis* and *T. sericea*).

Comparison of size class distributions between the two sites for each species indicated a significant change ($p < 0.001$) in size class distribution for all but one species, that being *C. collinum*.

The quotient plots indicated that some populations were stable (Figure 1), but others not so, irrespective of management regime. Thus, for the protected site, three populations appeared to be relatively stable (*C. collinum, S. madagascariensis* and *T. sericea*), and three were unstable (*A. swazica, D. cinerea* and *M. senegalensis)*. The three species with unstable population structures have been regarded as relatively aggressive bush encroacher species (Bredenkamp 1986). For populations in the communal land, the quotient curves indicated that two species had a stable population [*D. cinerea* and *T. sericea* (except for the larger size classes)]. The remaining four species at the communal site were all characterized by apparently unstable populations. Thus, *T. sericea* was the only species that had a stable population at both sites, *M. senegalensis* had an unstable population at both sites, and the results for the other three species common to both sites were inconsistent between sites.

There were significant differences in the mean density of seedlings for each species ($p < 0.001$), except for *S. madagascariensis* where the two values were similar (Table 2). Seedling densities of *T. sericea* and *M. senegalensis* were markedly increased in the communal land relative to the protected site, whilst the densities for *C. collinum* and *D. cinerea* were significantly reduced. However, because there were significant differences in the total number of stems, irrespective of size, for all the species between the two sites, the relative proportion of seedlings is a better index. This indicates that the number of seedlings per population is greatly increased in the communal land, except for *C. collinum*, and could be interpreted as the initial stages of bush encroachment (Tainton 1992; Teague & Smit 1992), possibly a result of the high grazing pressure (Skarpe 1990).

Discussion

It is significant that for the five species recorded at both sites, the shape of the density curves at the two sites were dissimilar for a given species, with the sole exception of *T. sericea* (a reversed J-shaped curve at each site). Moreover, while most of the density distributions for species in the protected site conformed to one of a range of standard distributions, those from the communal site often did not, or demonstrated modified standard curves. For example, *L. camara* exhibited a truncated rotated sigmoid, *C. collinum* was characterized by a flattened reversed J-shaped curve, and *D. cinerea* and *S. madagascariensis* had a direct linear decrease. This is contrary to the findings of Rao *et al.* (1990), who reported a decreased range of curve types in disturbed sites relative to undisturbed sites. Assuming that the distribution for each species in the protected site is what could be expected in the absence of major disturbance, it is clear that communal management has markedly altered the size class distributions, as well as density. This was substantiated by the chi-squared analyses.

The quotient plots indicated that eight of the twelve populations examined were unstable, with variable transitions from one size class to the next. It is noteworthy that the populations that did appear to be stable, were of species that can attain relatively large size classes, namely *C. collinum, S. madagascariensis* and *T. sericea*. The exception was the *D. cinerea* population in the communal land. Otherwise the populations of the more shrubby species, and the tree species in the communal land, appeared to be unstable. Quotient plots from other southern African studies have also shown that most species demonstrate unstable populations (Taylor & Walker 1984; Walker *et al.* 1986).

The density distribution curves also facilitate some inferences about the relative stability or instability of the various populations. A stable population is characterized by low ratios of change between successive size classes (Taylor & Walker 1984), corresponding to marginally convex curves without clear inflections (Knowles & Grant 1983). Most of the curves for this study do not conform to this ideal. A variety of curve shapes were found with the curve of the protected area generally being above that of the communal area, except for *M. senegalensis*. The initial steep slopes of the smaller size classes indicate a large increment of change in contrast to the relatively flat slopes of the larger size classes. This indicates a low rate of change in mortality rate in the larger age classes. The elongated tail of the curve is truncated for data from the communal site. Thus, it appears that the depicted size classes represent unstable populations.

The plots of quotients show variable recruitment at both sites for most of the species. This is to be expected in semi-arid savanna areas with fluctuating climates, fire, herbivory and human impact. Consequently, it is difficult to attempt to project population trends other than in the short term. Exceptions are *T. sericea* at both sites, and *S. madagascariensis* and *C. collinum* at the protected site.

Communal management appears to have had a marked impact on the proportional size class distribution of most of the species discussed here, other than *C. collinum* and *T. sericea*, although even for these two species, densities in each size class were clearly reduced. This has usually been through a reduction in the number of size classes present, and a reduction in the proportion of the population in the larger size classes. Additionally, it has promoted a species-

Table 2 Seedling densities (number/ha ± SE), and percentage of seedlings of the dominant woody species at the protected ($n = 30$) and communal ($n = 40$) areas

	Density		Percentage	
Species	Protected	Communal	Protected	Communal
A. swazica	40.8 ± 10.8	—	13.4	—
C. collinum	37.5 ± 22.4	3.8 ± 2.1	12.8	11.4
D. cinerea	93.3 ± 16.3	45.0 ± 11.4	7.6	18.3
L. camara	—	23.8 ± 10.7	—	6.4
M. senegalensis	35.8 ± 14.0	115.0 ± 37.2	16.7	20.3
S. madagascariensis	20.8 ± 7.8	24.4 ± 9.2	6.5	68.2
T. sericea	258.3 ± 54.9	1076.9 ± 234.6	23.1	35.6

specific reduction in absolute density. This reduction is marked for larger individuals of *C. collinum*, *D. cinerea* and *S. madagascariensis*. This is noteworthy, since the larger size classes are currently not the size classes preferred for fuelwood purposes (Shackleton 1993). It is possible that the size classes currently selected for fuelwood are not the most desirable, but are the most frequently encountered now that the larger individuals are absent. However, this is unlikely since the larger individuals are probably too large for easy harvesting, transporting and handling as fuelwood. Nor do fuelwood collectors significantly favour the larger size classes (relatively) that are still in abundance. Thus, it is unlikely that these have been removed as a consequence of fuelwood demand. However, large posts are used extensively for fencing, and this is probably a major contributor to the removal of the larger size classes. Skarpe (1990) recorded a reduction in the range of height classes present with increasing disturbance in an arid savanna in Botswana.

The gradual reduction of the range of size classes present in the communal lands could be a reason for concern and has management implications even if the harvesting pressure is reduced. Removal of the harvesting pressure will result, in the medium to long term, in the development of relatively even-aged stands of each species, until they reach maturity. Thereafter, new cohorts of seedlings will be established at regular intervals leading to a standard size class distribution. Even-aged stands are undesirable, since particular developmental stages may be more prone to environmental disturbance, stress or disease, than others. If most of the population is in that developmental stage there may be a simultaneous loss of the whole cohort (Harper 1977). This may be from natural senescence, harvesting or may be induced through some external stress (Young & Lindsay 1988).

Two of the three species favoured for fuelwood (*A. swazica* and *C. collinum*) have experienced a decrease in both absolute and relative density in the communal area. The third favoured species, *T. sericea*, experienced an increase. Similarly, two of the unfavoured species (*L. camara* and *M. senegalensis*) have experienced an increase in the communal area, whilst *S. madagascariensis* did not. Clearly, fuelwood rating alone is inadequate to explain or predict the observed changes in abundance of individual species. Other attributes, such as growth rate and coppice response to harvesting, need to be considered as well. Thus, it can be hypothesized that species likely to diminish in abundance would be those highly favoured as fuelwood, with a slow growth rate and weak coppicing ability. Species that are likely to increase under such a management regime would be those unattractive as fuelwood, with a relatively fast growth rate. This needs to be investigated.

Changes in the size class profile and a reduction in species-specific density at the communal site may ultimately lead to a reduction in species richness. The absence of *A. swazica* is an example of the removal of what was presumably a relatively common species. The densities of each of *C. collinum*, *D. cinerea* and *S. madagascariensis* in the communal area have been reduced to less than 20% of those recorded in the protected area. In total, there were 20 fewer species recorded at the communal site than at the protected site (Shackleton 1993). However, it is not possible to extrapolate possible rates of total species loss, since removal of some species obviously favours the increase or introduction of others. This is exemplified by the fact that although there was a significant reduction in the density of particular species, this does not apply to the total density (Shackleton 1993). Differential species responses add to the uncertainty related to the merits, or opposite, of prohibitive legislation as a means of overseeing the use of communal lands until the dynamics of individual species are more closely understood.

This study has indicated that stability of woody populations is probably rarely attained in an environment typified by large climatic fluctuations, even under low fire, herbivore and harvesting pressures. It appears a contradiction of terms that stability can be inferred from projections of size class distributions if the absolute densities are declining from sustained harvesting pressure. Although the size class profile is uniform, if harvesting pressure across the different size classes is proportional to relative densities in each size class, then there will be no change in the size class distribution at a time when absolute densities are declining. Therefore, although a case has been made for structural analysis to complement species compositional analysis, it should be related to trends in absolute densities and vice versa.

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